Being at the right place at the right time

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Chapter 3

Persistent small-scale demographic structure suggests cryptic despotic behavior in a flocking shorebird during the nonbreeding season

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Abstract

When all individuals have similar habitat requirements and are not constrained in their movements, sexes and ages are predicted not to segregate. In the gregarious red knot *Calidris c. canutus* wintering at Banc d'Arguin, Mauritania, West Africa, mark-resighting data of 1,606 birds over eight winters showed persistent age and sex segregation between two high-tide roost sites only three km apart. One site had a higher proportion of males (58% vs. 48%) and juveniles (45% vs. 22%) than the other. Movements between sites occurred infrequently, and were three times as frequent from the 'male/juvenile' to the 'female/adult' site as the reverse. Adult survival was three percentage-points higher at the 'female/adult' site (0.84 ± 0.01 SE) than at the 'male/juvenile' site (0.81 ± 0.03), where food abundance was higher because of the denser seagrass beds available. This demographic structuring may be driven by despotic behavior (females are larger) including arrival time differences (female return first) and a learning effect to handling high quality but potentially poisonous prey (juveniles moved more frequently). If arrival time plays a role, reproductive failure in the High Arctic would enable males to return earlier to tropical West Africa and thus 'compensate' by settling in the better areas.

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Introduction

Selecting a good area to live is crucial to all animals, as individuals that occupy sites with greater foraging success and lower predation danger would have higher survival and higher reproductive success, i.e. achieve higher fitness (Fretwell & Lucas 1969). This is no less true for seasonally migrating animals that show drastic shifts in habitat, with the caveat that what happens in one place could well affect what is possible in another (Harrison et al. 2010). Documenting and understanding such so-called 'carry-over' mechanisms is crucial when attempting to determine in which areas and during which time of the year a population is bottlenecked (Runge & Marra 2005, Buehler & Piersma 2008).

The null model for site occupancy by individual animals attempting to maximize fitness is the ideal-free distribution (IFD; (Fretwell & Lucas 1969, Fretwell 1972). The predictions of the IFD for equal competitors are that no individual can improve fitness by changing between areas. Assumptions of the ideal-free distribution are two-fold: animals know where to settle (in habitats where fitness rewards are highest, i.e. the animals are 'ideal') and individuals are not constrained in their movements (e.g. by despotic behavior or travel costs, i.e. the animals are 'free') (Fretwell & Lucas 1969, Fretwell 1972). When some animals are more equal than others, i.e. not 'free' but still 'ideal', they would converge to the ideal-despotic distribution (Fretwell 1972).

Shorebirds tend to occupy open wetland habitats especially during the nonbreeding season. They are a profitable group in which to study spacing and social behavior in relation to food availability, predation pressure, traveling costs, and competition (Myers 1984, van de Kam et al. 2004). Whereas in some species some individuals may show clearly despotic behavior such as defending feeding territories (Turpie 1995, Johnson et al. 2001), in other species interference is either absent, or cryptic, and such species tend live in flocks (Myers et al. 1979, Myers 1980). A good example of a densely flocking species with apparently low interference costs is the long-distance migrating red knot *Calidris canutus* (van Gils & Piersma 2004). During the nonbreeding season they forage socially in intertidal habitats and form flocks of up to several thousand individuals (Piersma et al. 1993b, Folmer et al. 2010). Based on interpreted distribution patterns over a variety of spatial and temporal scales, red knots have been shown to behave as if they are both ideal and free (across all western European coastal wetlands over a whole winter when costs of moving were low in relation to distance traveled; Quaintenne et al. 2011), or ideal but not free (across a single wetland site over a week when costs of moving were relatively high; van Gils et al. 2006b).

Red knots breed circumpolar on the High Arctic tundra. Outside the breeding season they are found at coastal sites offering extensive mollusk-rich intertidal habitats in both the northern and southern hemisphere (Piersma et al. 2005, Piersma 2007). Although females are slightly larger than males, the differences are so small that red knots appear monomorphic and require molecular sexing (Dick et al. 1976, Baker et al. 1999). Unlike more dimorphic sandpiper species such as western sandpipers *Calidris mauri* (Fernández & Lank 2006), in red knots sexes and ages are not known to feed on different prey, nor to favor different habitats.

Here we report sex- and age-related differences in site use by red knots *C. c. canutus* at a tropical West African wintering site, the Banc d'Arguin, Mauritania. Using mark-resighting data and multi-state models, we estimate rates of movements between areas and area-specific survival rates. This leads us to propose that even in gregarious species as red knots subtle intraspecific competition may exclude particular classes of individuals from sites where food is most abundant and survival is highest.

Methods

Study area, catching and marking methods

The study site at Iwik Peninsula is a small section of Banc d'Arguin, the main nonbreeding grounds of the canutus subspecies (Piersma et al. 1992). During the 8-year study, catching and resighting efforts were conducted during 3-week expeditions in November/December of 2002 – 2009. Using mist-nets, red knots were captured at two high-tide roosts: Abelgh Eiznaya (19°54'N, 16°19'W) and Baie d'Aouatif (19°54'N, 16°17'W) around new moon spring-tides. In this study we include data from 1,606 birds individually marked with unique combinations of color-bands (see Appendix 3.A). Of these, 1,292 different individuals were resighted after release yielding a total of 1,544 observations (for details on observation efforts see Appendix 3.A).

Biometric and demographic parameters

Red knots were aged according to Prater et al. (1977), distinguishing hatch-year birds (juveniles, 3-6 months) from older birds (adults, > 12 months). We recorded bill (culmen) length (calipers; ± 0.1 mm), wing length (ruler; ± 1 mm), and tarsus length (calipers; ± 0.1 mm). Body mass was measured within four hours of capture (electronic scales; ± 1 g). A blood sample of 5-20 µl was collected from the brachial vein and stored in 96% ethanol for molecular sexing (Baker et al. 1999, Appendix 3.A).

We used binomial logistic regression to test for differences in sex (females:males) or age (juveniles:adult) ratios between the two sites, using site as a factor.

We used linear regression models with sex, age and site (as factors) as explanatory variables to assess potential differences in structural body size or body mass. As body mass can vary as a consequence of individual variation in size or in nutritional stores (van der Meer &Piersma 1994), wing, tarsus and bill length measurements were analyzed in a Principal Component Analysis (PCA). PC1 explained 58% of the variation on structural body size. The residuals of a linear regression model of body mass against PC1 were used to compare differences in body stores between the two sites (ß ± SE: 5.04 ± 0.16, $t = 31.83$, $p < 0.001$; n = 1,606). We selected the most parsimonious model by stepwise deleting higher interaction and other non-significant terms. We used R 2.10.1 statistical software (R Development Core Team 2008).

Capture and resighting data were combined to create encounter histories for estimating demographic parameters with multi-state models (Arnason 1973, Nichols & Kendall 1995). Multistate models offer site-specific estimates of annual apparent survival Φ (phi), and movement among sites (transition) Ψ (psi), corrected for site-specific encounter rates *p*. Detections of red knots in the encounter histories were coded by site (A=Abelgh Eiznaya, B=Baie d'Aouatif, 0=not seen), and the site-specific transition parameters ($\Psi^{A\text{-}B}$, $\Psi^{B\text{-}A}$) described the probabilities of movement for individuals switching between the two sites. Because multi-state models have a large number of parameters, we made three a priori assumptions to reduce parameter number and increase parameter precision. Observation effort differed among years and sites, and we included these factors but not sex or age in modeling *p* (see Appendix 3.A). We were less interested in annual variation within our relatively short time series, and Φ and Ψ were modeled as constant over time, but we tested for differences between sexes, age classes and sites (Appendix 3.A). Earlier analyses of a data subset of the study population indicated that a time-since-marking (tsm) effect explained most of the variation in annual survival (Chapter 8), and we included tsm effects to control for transients or handling effects on Φ (Sandercock 2006). The probability of movement Ψ is conditional upon survival, and we tested age differences only for Φ. For more decision rules see Appendix 3.A.

The global model for testing the goodness of fit was $\Phi_{tsm+sex+age+site}\ \Psi_{sex+site+age}\ p_{site+time}$, using the median-ĉ (c-hat) test implemented in the MARK software (White & Burnham 1999). The estimated ĉ was 1.03 ± 0.00 SE, and ĉ was adjusted accordingly. Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc). The candidate model set consisted of all plausible combinations of parameterizations for Φ, Ψ and *p* (Appendix 3.B, table 3.B1). All models were constructed using design matrices and the logit link function in Program MARK (ver. 6.0,White & Burnham 1999). We used the model averaging function in MARK to calculate survival, transition and resighting probability and present parameter estimates as $\hat{\theta} \pm 1SE$.

Results

Catches of red knots at the Baie d'Aouatif high-tide roost included more males (58 ± 2% S.E.) and more juveniles (45 ± 8%) than the roost at Abelgh Eiznaya (males: 48 ± 3%, ß ± SE: -0.41 ± 0.11, z = -3.58, p = < 0.001; juveniles: 22 ± 6%, ß ± SE: -0.74 ± 0.12, z = -6.21, p = <0.001: both n = 8 winters, figure 3.1)

Overall, females were distinctly larger than males (for details see table 3.1, Appendix 3.C table 3.C1). Females had larger bills (t = -29.19, p < 0.001) and tarsi (t = -9.77, p < 0.001) than males. Adult females had longer wings than adults males and juvenile females and males, adult males had longer wings than juveniles females and males, and juvenile females had longer wings than juvenile males (t = -2.2, p = 0.028). Females were heavier than males (t = -11.9, p < 0.001), both in adults and juveniles (t = 7.7, p < 0.001). Between site differences additional to differences between the sexes were found in bill and tarsus length, with red knots having longer bills (t = 3.13, p = 0.002) and longer tarsi (t = 2.02, p = 0.04) at Abelgh Eiznaya than at Baie d'Aouatif.

Table 3.1 Wing [mm], bill [mm], tarsus length [mm] and body mass [g] (average ± s.d.) of wintering red knots were tested in linear regression models for effects of sex, age and/or catching location (site) Abelgh Eiznaya and Baie d'Aouatif. Each letter indicates significant different groupings (p < 0.01, for all relevant parameters see table 3.C1). n = sample size for Abelgh Eiznaya (A) and Baie d'Aouatif (B) respectively. Regressions on body mass were tested on size corrected body mass.

		adults		juvenile	
		female (n: A = 454; B = 86)	male (n: A = 355; B = 111)	female (n: A = 135; B = 72)	male (n: A = 164; B = 98)
wing [mm]	Abelgh Eiznaya	174 ± 4[a]	169 ± 4[b]	167 ± 4[c]	163 ± 3[d]
	Baie d'Aouatif	174 ± 4[a]	169 ± 4[b]	167 ± 3[c]	163 ± 3[d]
bill [mm]	Abelgh Eiznaya	36.2 ± 1.73[a]	34.5 ± 1.62[c]	36.4 ± 1.65[a]	34.2 ± 1.41[c]
	Baie d'Aouatif	36.0 ± 1.72[b]	34.4 ± 1.75[d]	35.9 ± 1.65[b]	33.9 ± 1.62[d]
tarsus [mm]	Abelgh Eiznaya	33.0 ± 1.36[a]	32.5 ± 1.20[c]	33.0 ± 1.17[a]	32.3 ± 1.05[c]
	Baie d'Aouatif	33.0 ± 1.30[b]	32.0 ± 1.30[d]	33.0 ± 1.16[b]	32.3 ± 1.21[d]
body mass [g]	Abelgh Eiznaya	131 ± 8[a]	120 ± 8[b]	125 ± 8[c]	113 ± 9[d]
	Baie d'Aouatif	130 ± 7[a]	119 ± 7[b]	124 ± 10[c]	112 ± 9[d]

F statistics: wing: $F_{3,1471}$=525.2, r^2=0.52, p<0.001; bill: $F_{2,1472}$=236.9, r^2=0.24, p<0.001; tarsus: $F_{2,1472}$=51.9, r^2=0.06, p<0.001; body mass: $F_{2,1472}$=109.7, r^2=0.13, p<0.001

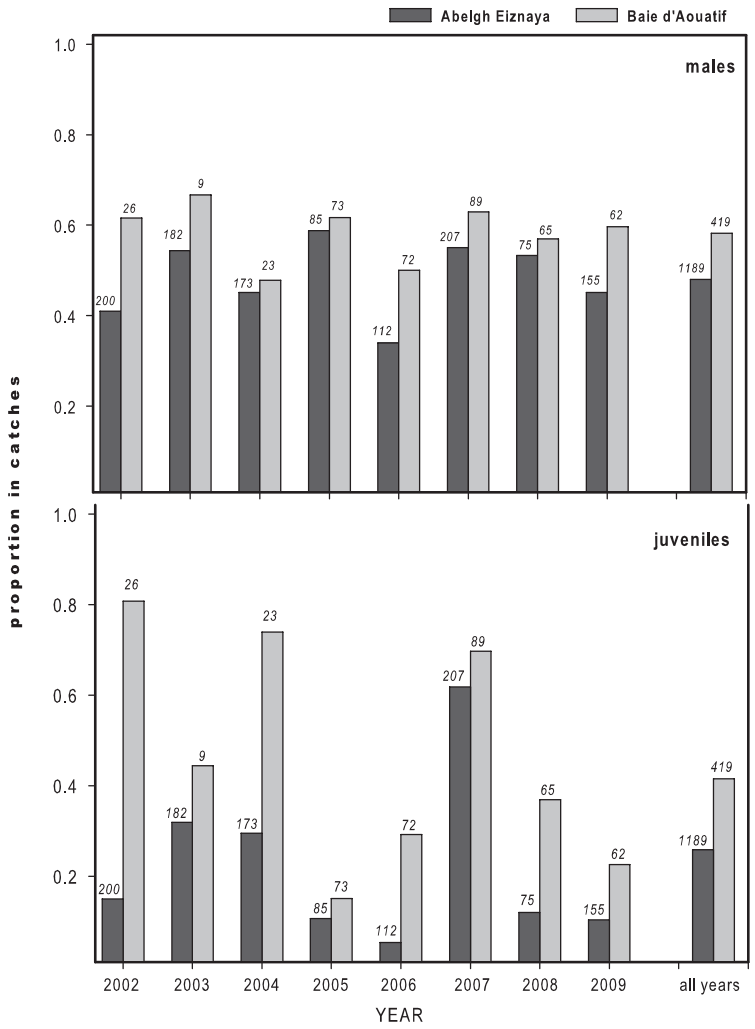


Figure 3.1 Proportions of males and juveniles among captures at Baie d'Aouatif and Abelgh Eiznaya, November-December 2002 to 2009. Numbers in italics indicate the numbers of red knots examined.

Table 3.2 The most parsimonious multi-state models (ΔQAICc < 2) estimated apparent annual survival Φ and movement probability ψ depending on time-since-marking (tsm), age-class (age: adult/juvenile), sex (male/female) and site (Abelgh Eiznaya/Baie d'Aouatif) for red knots at Iwik Peninsula, Banc d'Arguin, Mauritania, West Africa, in winters 2002 – 2009. Resighting probability *p* was exclusively modeled depending on site and time (year). For a list of all tested models see Appendix 3.B, table 3.B1.

Model	NP	QDeviance	QAICc	Δ QAICc	QAICc weight
$\phi_{tsm+site}\ \psi_{age+site}\ p_{site+time}$	14	1553.59	6568.48	0	0.098
$\phi_{tsm+age+site}\ \psi_{age+site}\ p_{site+time}$	15	1552.38	6569.29	0.81	0.065
$\phi_{tsm+site}\ \psi_{site}\ p_{site+time}$	13	1556.47	6569.34	0.86	0.064
$\phi_{tsm}\ \psi_{age+site}\ p_{site+time}$	13	1556.52	6569.38	0.90	0.062
$\phi_{tsm+age}\ \psi_{age+site}\ p_{site+time}$	14	1554.92	6569.81	1.32	0.050
$\phi_{tsm+site}\ \psi_{age+sex+site}\ p_{site+time}$	15	1553.17	6570.09	1.60	0.044
$\phi_{tsm+age+site}\ \psi_{site}\ p_{site+time}$	14	1555.25	6570.14	1.66	0.043
$\phi_{tsm}\ \psi_{site}\ p_{site+time}$	12	1559.34	6570.19	1.71	0.042
$\phi_{site}\ \psi_{age+site}\ p_{site+time}$	13	1557.33	6570.20	1.71	0.041
$\phi_{tsm+site}\ \psi_{age+site}\ p_{site+time}$	15	1553.59	6570.51	2.02	0.036

Model statistics include: number of parameters (NP), Deviance, Akaike's information criterion corrected for small sample size (QAICc), ΔQAICc, and QAICc weight. The goodness of fit was tested for the biologically most significant full model $\Phi_{tsm+age+sex+site}\ \psi_{age+sex+site}\ p_{site+time}$ and ĉ was adjusted to 1.03 ± 0.00.

The probability of encounter *p* increased among years at both sites (table 3.2). Nine models differed in ΔAICc < 2, describing variations in Φ as a function of tsm, site and/or age and variations in ψ as a function of site, age and/or sex (table 3.2; for a list of all tested models see Appendix 3.B, table B1). At both sites, adult survival was lower in the first year after marking than subsequent years, and survival was lower at Abelgh Eiznaya ($\Phi^1 = 0.79 \pm 0.03$ (95% CI = 0.74 – 0.84); $\Phi^{2+} = 0.84 \pm 0.01$ (0.81 – 0.86), table 3.3) than at Baie d'Aouatif ($\Phi^1 = 0.76 \pm 0.03$ (0.69 – 0.82); $\Phi^{2+} = 0.81 \pm 0.03$ (0.75 – 0.86)). The probability of switching sites was low overall, but directional movements of adults were less frequent from Abelgh Eiznaya to Baie d'Aouatif ($\psi^{A\rightarrow B} = 0.06 \pm 0.01$ (0.05 – 0.08)) than in the opposite direction ($\psi^{B\rightarrow A} = 0.18 \pm 0.02$ (0.15 – 0.23)). Juvenile survival was slightly lower than adult survival and movements were more frequent, showing the same directionality as adults (table 3.3).

Table 3.3 Model estimates of annual apparent survival (Φ), movement (ψ) and resighting probability (*p*), standard errors (SE), and 95% confidence intervals (CI) for eight years of measuring red knots at their tropical wintering area Banc d'Arguin, Mauritania, West Africa. 2002 - 2009. Results shown are for the top-supported model only (table 3.2). Apparent annual survival Φ showed a time-since-marking effect and differed slightly between sites. Φ^1 denotes apparent survival in the first year after marking, Φ^{2+} denotes apparent survival in subsequent years. Movement ψ was preferential from Baie d'Aouatif to Abelgh Eiznaya. Resighting probability p differed among years and between sites. Other models within ΔAICc units <2 differed in one parameter only and did not explain further variation significantly better.

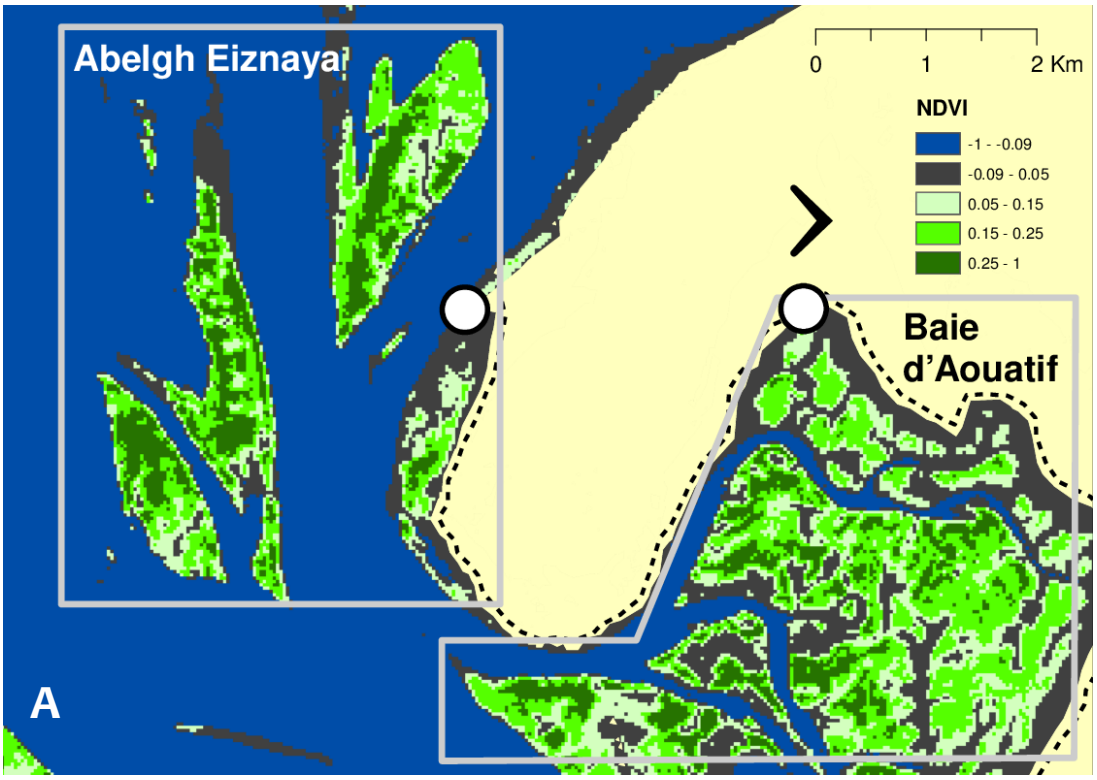
estimate ± SE	95% CI				
	Abelgh Eiznaya			Baie d'Aouatif	
annual apparent survival ϕ					
ϕ^1	0.79 ± 0.03	0.74 - 0.84		0.76 ± 0.03	0.69 - 0.82
ϕ^{2+}	0.84 ± 0.01	0.81 - 0.86		0.81 ± 0.03	0.75 - 0.86
movement ψ					
ψ	0.06 ± 0.01	0.05 - 0.08	→ move to →		
			← move to ←	0.18 ± 0.02	0.14 - 0.23
resighting probability *p*					
2003	0.30 ± 0.04	0.23 - 0.38		0.25 ± 0.05	0.17 - 0.35
2004	0.38 ± 0.03	0.32 - 0.44		0.32 ± 0.04	0.24 - 0.42
2005	0.45 ± 0.03	0.40 - 0.50		0.40 ± 0.05	0.31 - 0.49
2006	0.55 ± 0.03	0.49 - 0.60		0.49 ± 0.04	0.41 - 0.57
2007	0.61 ± 0.03	0.55 - 0.66		0.55 ± 0.04	0.47 - 0.63
2008	0.51 ± 0.03	0.46 - 0.56		0.46 ± 0.04	0.38 - 0.53
2009	0.58 ± 0.03	0.51 - 0.64		0.52 ± 0.04	0.44 - 0.60
juvenile ϕ	0.78 ± 0.04	0.70 - 0.84		0.75 ± 0.04	0.66 - 0.82
juvenile ψ	0.08 ± 0.02	0.05 - 0.14 →		← 0.22 ± 0.05	0.14 - 0.33

Discussion

We documented consistent sex and age segregation between the two sites in all eight years of study. As previously documented (Dick et al. 1976, Tomkovich & Soloviev 1996), structural body size and body mass mostly differed between the different sex/age categories, but despite being statistically significant, the absolute differences were small and variance was high, hence the need of molecular methods to reliably sex red knots (Dick et al. 1976, Baker et al. 1999). Yet, the older (more experienced) age-class (adults) and the generally larger sex (females) formed the majority at Abelgh Eiznaya, where individuals also had the longer bills and tarsi even when accounting for sex. Confirming a previous study showing high site-faithfulness within a winter season (Leyrer et al. 2006), there was little interchange between the high tide roosts of Abelgh Eiznaya and Baie d'Aouatif, despite the two being only three km apart. Red knots routinely migrate some 20,000 km each year and the lack of movements between the two sites suggests that individual red knots somehow were restrained from moving freely. Those individuals that did move switched from the male/juvenile dominated (Baie d'Aouatif) to the female/adult dominated (Abelgh Eiznaya) site, to where birds also had a higher annual survival.

The following suggests that the main reason why Abelgh Eiznaya provided higher survival is that it offered better foraging conditions. The intertidal flats at Banc d'Arguin include two main types of foraging habitat: seagrass meadows (predominantly *Zostera noltii*) alternate with bare sandy flats (Wolff & Smit 1990). red knots preferentially feed on dense muddy seagrass (Altenburg et al. 1982), a habitat that harbors higher densities of mollusk prey (Honkoop et al. 2008) and offers higher intake rates (J.A. van Gils, unpubl. data) than the sandy area flats. Landsat satellite images for the years of our study showed that the foraging areas of Abelgh Eiznaya (an assessment made based on Leyrer et al. 2006) provided denser seagrass coverage than the foraging areas in the Baie d'Aouatif (figure 3.2, Appendix 3.D) and thus better foraging opportunities. In contrast to strongly dimorphic migratory shorebirds such as the western sandpipers (Fernández & Lank 2006), red knots have never been shown to segregate among habitats with respect to external morphological traits. Instead, only gizzard size explained differential foraging distributions (van Gils et al. 2005b). Eating hard-shelled mollusks that need to be crushed and processed internally, gizzard size constrains the rate of food intake. Thus, the interaction between prey quality and gizzard size is a central determinant in foraging patch choice (van Gils et al. 2005b). Gizzard size is a plastic trait (Dekinga et al. 2001), and growth and maintenance of a large gizzard takes time and energy (reviewed in van Gils et al. 2007). Consistent with the idea that individual red knots that move from Baie d'Aouatif to Abelgh Eiznaya will do better, at least in terms of foraging, the gizzards of red knots roosting at Abelgh Eiznaya in April 2007 – 2009 (measured by ultrasonography; Dietz et al. 1999) were slightly smaller (8.79 g ± 2.86; n = 9) than at Baie d'Aouatif (10.45 g ± 3.44; n = 77; t-test: $t = 1.607$, df = 10.907, $p = 0.1366$). In addition, Abelgh Eiznaya may be safer, as observations on foraging red knots indicate a lower predation risk (M. van der Geest, J.A. van Gils unpubl. obs.).

Under the IFD we would not have expected survival differences between areas. The predominant movement to the better quality area between winters suggests though that the red knots were well aware of the quality differences. In the following we present three non-mutually exclusive hypotheses potentially explaining the observed movement patterns. In the first place, the difference between the two roost sites could reflect a buffer effect (Kluyver & Tinbergen 1953, Brown 1969, Gill et al. 2001). Since the larger (females) and older birds occurred mostly at the site with the higher survival, we suggest that some type of despotism maintains the sex- and age-related structuring. As females are not only slightly larger, but also return first from the High Arctic



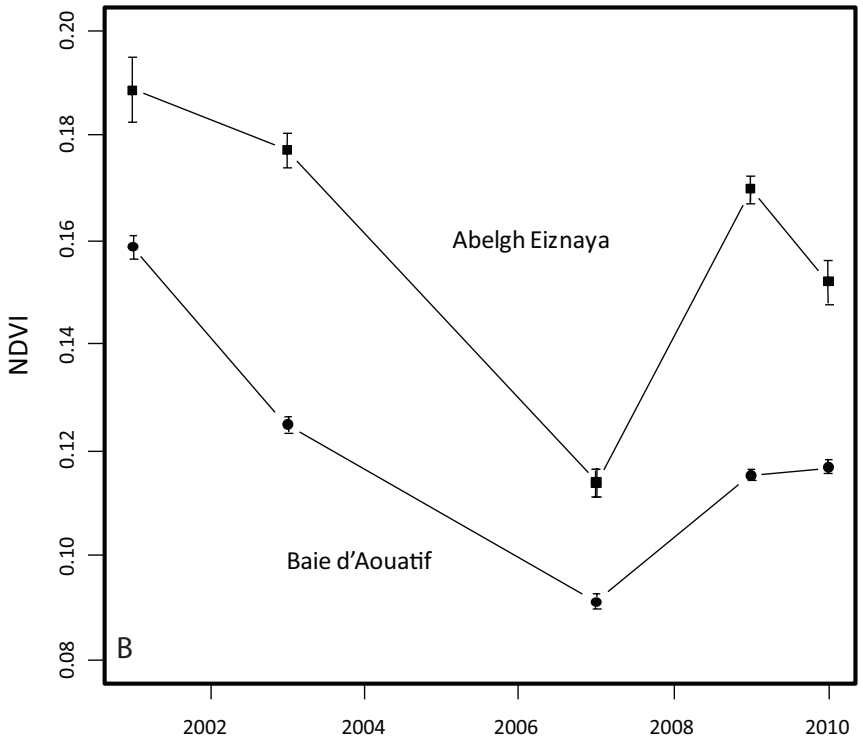


Figure 3.2 A The distribution of seagrass beds in the intertidal foraging area of red knots at Banc d'Arguin, Mauritania, shown as variances in 'Normalized Differences Vegetation Indices' NDVI intensities obtained from five suitable Landsat images (Appendix 3.D, J.A. van Gils, unpubl data). Yellow areas show mainland, blue areas show water, grey areas show bare intertidal mudflats, and green colors indicate various NDVI intensities (see legend). Grey-bordered blocks indicate intertidal foraging areas connected to the respective high tide roosts. **B** NDVI values (mean ± SE) plotted over time for both foraging areas. NDVI values for the foraging areas were higher for Abelgh Eiznaya (Student's $t = 6.2$, df = 4, $p < 0.005$), indicating that Abelgh Eiznaya offered better foraging conditions than Baie d'Aouatif.

breeding to the wintering grounds (Piersma et al. 1992, Tomkovich & Soloviev 1996, Nebel et al. 2000), the order of arrival could also play a key role in site occupancy. As the Afro-Siberian red knot population shows a declining trend (Davidson & Piersma 2009), we may have observed a net movement to the better site as slots become available. If this would be the case, we would expect a net movement towards Baie d'Aouatif as the population increases again.

A second hypothesis is based on recent observations that the preferred prey (*Loripes* ssp.) has high sulfur concentrations and thus could be poisonous prey (J.A. van Gils, unpubl. data). Adult red knots seem to be more resilient in dealing with high sulfur loads (T. Oudman, J.A. van Gils unpubl. obs.), which would support our observations that it was mainly adults that were found at the *Loripes* site Abelgh Eiznaya. We thus expect that red knots would move from Baie d'Aouatif to Abelgh Eiznaya in the course of their life, and this is indeed what seems to happen: juvenile red knots show an even higher likelihood to move there in the first year of their life than (later as) adults.

The third hypothesis is based solely on the timing of arrival back at Banc d'Arguin and the assumption that arrival time determines the resource holding potential of returning red knots. Successfully reproducing males attend their offspring for almost three weeks after females have left the High Arctic (Tomkovich & Soloviev 1996), even though females are physiologically perfectly capable to give this care if experimentally forced to do so (Pierce et al. 2010). One reason could be that females profit from arriving early in the nonbreeding grounds. On their way south, female *canutus* red knots, but not males, appear to stage in the Wadden Sea for a 2-3 week period (Nebel et al. 2000). Instead, *canutus* males may routinely accomplish a 9,000 km nonstop southward migration yet, still arrive later than the females. In years when breeding is unsuccessful (see Meissner 2005), males may be able to catch up and arrive with the females. This might enable some of them to make a move to a better wintering site, thus partially 'compensating' for reproductive failure. With the miniaturization of new tracking devices (e.g. Conklin et al. 2010), assessments of such trade-offs in individual life-histories of long-distance migrants will become within reach.

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Appendices

Appendix 3.A Sexing, marking and observation efforts and resighting probabilities

Red knots captured in 2002 – 2006 were sexed with primers P2/P8 (Griffiths et al. 1998) verified for red knots by Baker et al. (1999). To avoid sexing errors due to potential length polymorphisms in the Z-intron of the CHD gene (Casey et al. 2009, Schroeder et al. 2010), primers 2602F/2669R (Fridolfsson &Ellegren 1999; modified for shorebirds by O. Haddrath, unpubl. data) were used from 2007 onwards.

For survival and movement analysis, 1,292 red knots were caught between 2002 and 2008 at the two neighboring high-tide roosts less than 3km apart at Banc d'Arguin, Mauritania, West Africa. The birds were individually marked with a numbered metal band of the Dutch ringing scheme ('Vogeltrekstation Arnhem') and a unique combination of four color-bands and a leg flag (Piersma & Spaans 2004). More red knots were caught at the Abelgh Eiznaya high tide roost (982 individuals) than at the Baie d'Aouatif high tide roost (310 individuals) (table 3.A1). These birds were followed in subsequent winters 2003 – 2009. Juvenile red knots were considered as juveniles during their first year of life, and were treated as adults as they returned in subsequent years.

Abelgh Eiznaya — individuals (moved)

YEAR	2002	2003	2004	2005	2006	2007	2008	2009
newly ringed	**177**	41 (2)	45 (-)	51 (5)	51 (3)	44 (4)	22 (1)	23 (1)
%		*23*	*25*	*29*	*29*	*25*	*12*	*13*
		171	57 (10)	66 (3)	63 (12)	59 (6)	42 (4)	25 (4)
			33	*39*	*37*	*35*	*25*	*15*
			162	62 (4)	55 (3)	55 (3)	38 (-)	37 (3)
				38	*34*	*34*	*23*	*23*
				83	34 (4)	39 (5)	24 (2)	16 (-)
					41	*47*	*29*	*19*
					112	52 (8)	37 (3)	42 (8)
						46	*33*	*38*
						202	68 (6)	75 (14)
							34	*37*
							75	30 (7)
								40

Baie d'Aouatif — individuals (moved)

YEAR	2002	2003	2004	2005	2006	2007	2008	2009
newly ringed	**21**	5 (1)	2 (1)	2 (1)	4 (-)	1 (-)	2 (1)	—
%		*24*	*10*	*10*	*19*	*5*	*10*	*0*
		5	2 (1)	—	1 (-)	—	—	—
			40	*0*	*20*	*0*	*0*	*0*
			20	7 (4)	8 (2)	7 (5)	6 (5)	3 (2)
				35	*40*	*35*	*30*	*15*
				68	26 (4)	25 (7)	16 (7)	19 (4)
					38	*37*	*24*	*28*
					49	20 (4)	21 (3)	17 (4)
						41	*43*	*35*
						83	32 (6)	28 (6)
							39	*34*
							64	37 (3)
								58

Table 3.A1 Numbers of newly ringed red knots at the two study sites Abelgh Eiznaya and Baie d'Aouatif each year (bold numbers in first diagonal). In lines: total number of individuals re-sighted each year of the respective cohort. In brackets number of individuals that have been re-sighted at the other site in that year. Italic numbers: percentages of total numbers seen back per cohort and year.

The high tide roost that the birds were caught at was assigned as 'their' high tide roost. Observations made at 'the other' site were recorded as movement. More than 50% of the resighted individuals were seen more than one time and/or by more than one observer per year. Individu als that were not recorded for four consecutive years and then resighted for only one time were excluded from the analysis as potentially wrong readings. In the 73 (out of 1,544) cases when an individual was seen at both sites within one year, the site with the higher number of observations was selected and recorded as 'site of observation'. A few individuals that were seen within one year at both sites once only were excluded from the analysis. Of these excluded birds only three individuals were resighted at 'the other' site in subsequent years.

About 30 – 40% of the marked individuals of a cohort were resighted annually. Especially in later study years, sometimes more than 40% of a cohort were resighted. Occasionally, especially in the earlier study years, less than 30% were resighted (table 3.A1). The increase in observed individuals each year was mainly due to having more individuals marked in the population, but also due to improvements in resighting probabilities.

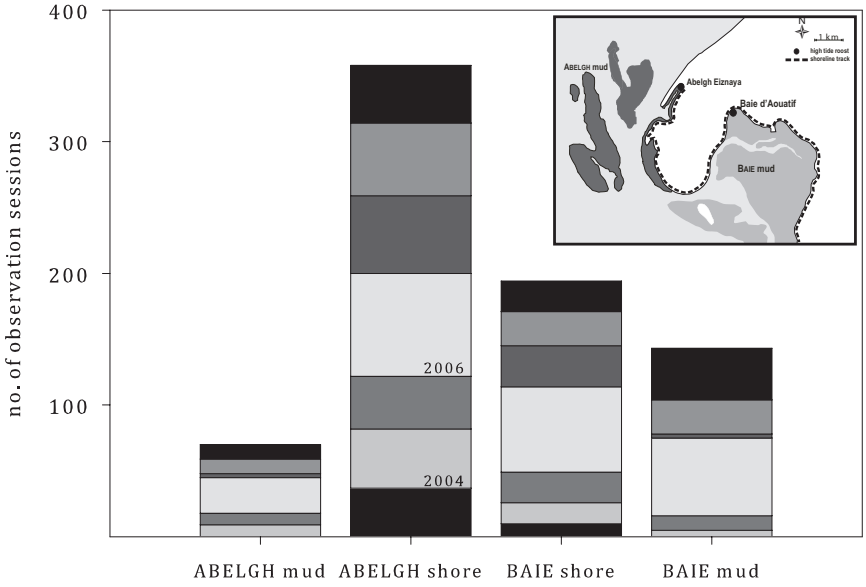

Figure 3.A1 Number of observation sessions per year and area. Abelgh Eiznaya is presented in dark grey, Baie d'Aouatif is presented in lighter grey, other grey shades indicate non-visited mudflats and water. Observations at mudflats away from shore in both areas started in 2004. An observation session is defined as the time (1 – 3 hrs) a single observer spent in an area.

Observations took place within three-week expeditions in November/December 2003 – 2009. On average, ten experienced color-band readers scanned the total study area along the shoreline track every day (figure 3.A1). From 2004 onwards, all inter-tidal mudflats not or hardly accessible from shore were visited by boat as often as weather and tidal conditions allowed. From 2007 onwards the use of snow rackets allowed much better walking on the soft mudflats and the observation radius could be improved once more.

Because numbers marked at the Baie d'Aouatif high tide roost were low in the beginning, Φ and ψ were not modeled as a function of differences in annual conditions. Yet, resighting probability p was modeled as a function of time, as logistic improvements suggested resighting effort to differ between years. The habitat used by red knots at Banc d'Arguin is mainly open mudflats and beaches without vegetation. Apart from apparently selecting different high tide roosts and foraging areas, behavior did not differ between the sex and age classes with foraging on the mudflats during low tide and assembling at the high tide roosts during high tide. There was no reason to expect p to differ between sex or age, consequently p was not modeled as a function of different behavior in sex or age classes within a site.

Appendix 3.B Multi-state candidate models

Table 3.B1 List of all candidate multi-state models tested to estimate demographic parameters for red knots at two nonbreeding sites at Iwik Peninsula, Banc d'Arguin, Mauritania, in winter 2002 – 2009. Annual apparent survival Φ, movement probability ψ and resighting probability *p* were modeled as functions of time-since-marking (tsm), age (adult/juvenile), sex (male/female), site (Abelgh Eiznaya/Baie d'Aouatif), time (year) and constant. Model statistics include: number of parameters (NP), QDeviance, Akaike's information criterion corrected for small sample size (QAICc) (noted at bottom of table for the best model), ΔQAICc, and QAICc weight. The full model (indicated with *) used to test the goodness of fit was built on some a priori assumptions based on existing knowledge about the study system, described in detail in the material and methods paragraph and in Appendix 3.A. Goodness of fit was tested using the median ĉ-test implemented in the MARK software, ĉ was adjusted to 1.03 ± 0.00. The most parsimonious models (ΔQAICc < 2) are shaded in grey.

Model	NP	QDeviance	Δ QAICc	QAICc weights
$\Phi_{tsm+age+sex+site}\,\psi_{age+sex+site}\,p_{site+time}$*	17	1551.95	4.43	0.01
$\Phi_{tsm+age+site}\,\psi_{age+sex+site}\,p_{site+time}$	16	1551.95	2.41	0.03
$\Phi_{tsm+age+sex+site}\,\psi_{age+site}\,p_{site+time}$	16	1552.38	2.84	0.02
$\Phi_{tsm+sex+site}\,\psi_{age+sex+site}\,p_{site+time}$	16	1553.17	3.63	0.02
$\Phi_{tsm+age+sex}\,\psi_{age+sex+site}\,p_{site+time}$	16	1554.46	4.92	0.01
$\Phi_{tsm+age+sex+site}\,\psi_{sex+site}\,p_{site+time}$	16	1554.88	5.34	0.01
$\Phi_{tsm+age+sex+site}\,\psi_{age+sex}\,p_{site+time}$	16	1590.16	40.62	0
$\Phi_{tsm+age+site}\,\psi_{age+site}\,p_{site+time}$	15	1552.38	0.81	0.07
$\Phi_{tsm+site}\,\psi_{age+sex+site}\,p_{site+time}$	15	1553.17	1.60	0.04
$\Phi_{tsm+site}\,\psi_{age+site}\,p_{site+time}$	15	1553.59	2.02	0.04
$\Phi_{tsm+age}\,\psi_{age+sex+site}\,p_{site+time}$	15	1554.48	2.91	0.02
$\Phi_{tsm+age+site}\,\psi_{sex+site}\,p_{site+time}$	15	1554.88	3.31	0.02
$\Phi_{tsm+age+sex}\,\psi_{age+site}\,p_{site+time}$	15	1554.90	3.33	0.02
$\Phi_{tsm+age+sex+site}\,\psi_{site}\,p_{site+time}$	15	1555.25	3.68	0.02
$\Phi_{tsm+sex}\,\psi_{age+sex+site}\,p_{site+time}$	15	1556.04	4.47	0.01
$\Phi_{tsm+sex+site}\,\psi_{sex+site}\,p_{site+time}$	15	1556.11	4.54	0.01
$\Phi_{tsm+age+sex}\,\psi_{sex+site}\,p_{site+time}$	15	1557.35	5.78	0.01
$\Phi_{tsm+age+site}\,\psi_{age+sex}\,p_{site+time}$	15	1590.16	38.59	0
$\Phi_{tsm+age+sex+site}\,\psi_{age}\,p_{site+time}$	15	1590.18	38.61	0
$\Phi_{tsm+sex+site}\,\psi_{age+sex}\,p_{site+time}$	15	1590.96	39.40	0
$\Phi_{tsm+age+sex}\,\psi_{age+sex}\,p_{site+time}$	15	1591.06	39.49	0
$\Phi_{tsm+age+sex+site}\,\psi_{sex}\,p_{site+time}$	15	1596.62	45.05	0
$\Phi_{tsm+site}\,\psi_{age+site}\,p_{site+time}$	14	1553.59	0	0.10
$\Phi_{tsm+age}\,\psi_{age+site}\,p_{site+time}$	14	1554.92	1.32	0.05
$\Phi_{tsm+age+site}\,\psi_{site}\,p_{site+time}$	14	1555.25	1.66	0.04
$\Phi_{tsm}\,\psi_{age+sex+site}\,p_{site+time}$	14	1556.08	2.49	0.03
$\Phi_{tsm+site}\,\psi_{sex+site}\,p_{site+time}$	14	1556.11	2.52	0.03
$\Phi_{tsm+sex+site}\,\psi_{site}\,p_{site+time}$	14	1556.47	2.88	0.02
$\Phi_{tsm+sex}\,\psi_{age+site}\,p_{site+time}$	14	1556.47	2.88	0.02
$\Phi_{site}\,\psi_{age+sex+site}\,p_{site+time}$	14	1556.91	3.32	0.02
$\Phi_{tsm+age}\,\psi_{sex+site}\,p_{site+time}$	14	1557.36	3.77	0.01
$\Phi_{tsm+age+sex}\,\psi_{site}\,p_{site+time}$	14	1557.73	4.14	0.01
$\Phi_{tsm+sex}\,\psi_{sex+site}\,p_{site+time}$	14	1558.93	5.33	0.01
$\Phi_{tsm+age+sex}\,\psi_{age}\,p_{site+time}$	14	1590.18	36.59	0
$\Phi_{tsm+site}\,\psi_{age+sex}\,p_{site+time}$	14	1590.97	37.38	0

continue next page

continuation

Model	NP	QDeviance	Δ QAICc	QAICc weights
$\phi_{tsm+sex+site}\ \psi_{age}\ p_{site+time}$	14	1590.98	37.39	0
$\phi_{tsm+age}\ \psi_{age+sex}\ p_{site+time}$	14	1591.08	37.48	0
$\phi_{tsm+age+sex}\ \psi_{age}\ p_{site+time}$	14	1591.09	37.50	0
$\phi_{tsm+sex}\ \psi_{age+sex}\ p_{site+time}$	14	1592.04	38.45	0
$\phi_{tsm+age+site}\ \psi_{sex}\ p_{site+time}$	14	1596.63	43.03	0
$\phi_{tsm+age+sex+site}\ \psi_{const.}\ p_{site+time}$	14	1596.63	43.03	0
$\phi_{tsm+age+sex}\ \psi_{sex}\ p_{site+time}$	14	1597.31	43.71	0
$\phi_{tsm+sex+site}\ \psi_{sex}\ p_{site+time}$	14	1597.65	44.06	0
$\phi_{tsm+site}\ \psi_{site}\ p_{site+time}$	13	1556.47	0.86	0.06
$\phi_{tsm}\ \psi_{age+site}\ p_{site+time}$	13	1556.52	0.90	0.06
$\phi_{site}\ \psi_{age+site}\ p_{site+time}$	13	1557.33	1.71	0.04
$\phi_{tsm+age}\ \psi_{site}\ p_{site+time}$	13	1557.75	2.13	0.03
$\phi_{tsm}\ \psi_{sex+site}\ p_{site+time}$	13	1558.97	3.35	0.02
$\phi_{tsm+sex}\ \psi_{site}\ p_{site+time}$	13	1559.30	3.69	0.02
$\phi_{site}\ \psi_{sex+site}\ p_{site+time}$	13	1559.87	4.26	0.01
$\phi_{site}\ \psi_{age+sex}\ p_{site+time}$	13	1586.57	30.96	0
$\phi_{tsm+site}\ \psi_{age}\ p_{site+time}$	13	1590.99	35.37	0
$\phi_{tsm+age}\ \psi_{age}\ p_{site+time}$	13	1591.10	35.49	0
$\phi_{tsm+sex}\ \psi_{age}\ p_{site+time}$	13	1592.07	36.45	0
$\phi_{tsm}\ \psi_{age+sex}\ p_{site+time}$	13	1592.08	36.46	0
$\phi_{tsm+age+site}\ \psi_{const.}\ p_{site+time}$	13	1596.63	41.01	0
$\phi_{tsm+age+sex}\ \psi_{const.}\ p_{site+time}$	13	1597.32	41.70	0
$\phi_{tsm+age}\ \psi_{sex}\ p_{site+time}$	13	1597.32	41.70	0
$\phi_{tsm+sex+site}\ \psi_{const.}\ p_{site+time}$	13	1597.66	42.04	0
$\phi_{tsm+site}\ \psi_{sex}\ p_{site+time}$	13	1597.66	42.05	0
$\phi_{tsm+sex}\ \psi_{sex}\ p_{site+time}$	13	1598.50	42.88	0
$\phi_{tsm}\ \psi_{site}\ p_{site+time}$	12	1559.34	1.71	0.04
$\phi_{site}\ \psi_{site}\ p_{site+time}$	12	1560.23	2.60	0.03
$\phi_{tsm}\ \psi_{age}\ p_{site+time}$	12	1592.10	34.46	0
$\phi_{site}\ \psi_{age}\ p_{site+time}$	12	1592.86	35.22	0
$\phi_{tsm+age}\ \psi_{const.}\ p_{site+time}$	12	1597.33	39.69	0
$\phi_{tsm+site}\ \psi_{const.}\ p_{site+time}$	12	1597.67	40.03	0
$\phi_{tsm+sex}\ \psi_{const.}\ p_{site+time}$	12	1598.51	40.87	0
$\phi_{tsm}\ \psi_{sex}\ p_{site+time}$	12	1598.53	40.90	0
$\phi_{site}\ \psi_{sex}\ p_{site+time}$	12	1599.70	42.06	0
$\phi_{tsm}\ \psi_{const.}\ p_{site+time}$	11	1598.54	38.88	0
$\phi_{site}\ \psi_{const.}\ p_{site+time}$	11	1599.71	40.05	0
$\phi_{const.}\ \psi_{const.}\ p_{site+time}$	10	1601.03	39.35	0

QAICc = 6568.48

Appendix 3.C Differences in body size and body mass of red knots Calidris canutus canutus *in their wintering area Banc d'Arguin, Mauritania, West Africa, in winters 2002 - 2009*

Table 3.C1 Summary tables of linear regression models, non-significant (interaction) terms were dropped and models rerun

		Estimate	Std. Error	t-value	p-value
wing[1]	intercept	167.18	0.27	625.88	<0.001
	sex	-3.97	0.36	-11.1	< 0.001
	age	7	0.21	22.29	< 0.001
	sex:age	-0.95	0.43	-2.2	0.028
bill[2]	intercept	35.95	0.1	360.96	<0.001
	sex	-1.84	0.09	-21.19	<0.001
	site	0.31	0.10	3.13	0.002
tarsus[3]	intercept	32.86	0.07	440.07	<0.001
	sex	-0.63	0.06	-9.77	<0.001
	site	0.15	0.08	2.02	0.04
body mass[4]	intercept	0.09	0.41	0.21	0.8
	age	3.23	0.42	7.7	<0.001
	sex	-4.64	0.39	-11.9	<0.001

The parameter estimates for sex are given for males in relation to females, for age: adults in relation to juveniles, for site: Abelgh Eiznaya in relation to Baie d'Aouatif.

[1] $F_{3, 1471}$=525.2, r^2=0.52, $p < 0.001$; [2] $F_{2, 1472}$=236.9, r^2=0.24, $p < 0.001$

[3] $F_{2, 1472}$ = 51.9, r^2=0.06, $p < 0.001$; [4] $F_{2, 1472}$=109.7, r^2=0.13, $p < 0.001$

Appendix 3.D Assessing differences in foraging conditions by means of satellite images

The extent and abundance of intertidal seagrass beds can be accurately assessed using satellite imagery, especially by calculating so called 'Normalized Difference Vegetation Indices' (NDVI; Ferguson & Korfmacher 1997, Mumby et al. 1997). Over the entire study period we found five suitable Landsat images (18 Dec 2001, 22 Jan 2003, 9 Jan 2007, 11 Sep 2009, and 17 Jan 2010; freely downloadable at http://landsat.usgs.gov), from which NDVI values were calculated for both sites (on the basis of pixels of 30 by 30 m). To make the images comparable, we applied so-called 'radiometric calibration' (Chander et al. 2009), using the image from 17 Jan 2010 as a reference.

opposite site:
Aerial photographs of Abelgh Eiznaya and the outer mudflats west of Iwik Peninsula. Photographs taken by EnHaut! Kite Aerial Photography.